HABITAT RELATIONSHIPS IN PASSERIFORM BIRDS IN EASTERN NEW BRUNSWICK

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HABITAT RELATIONSHIPS IN PASSERIFORM BIRDS IN EASTERN NEW BRUNSWICK

by

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ABSTRACT

This study examined two aspects of breeding habitat selection in several species of migratory passeriform birds: (1) Quantitative bird-vegetational relationships and (2) philopatry of individuals to the breeding location.

In an attempt to discover vegetational characteristics to which species were responding, 19 variables of vegetational structure were measured and subjected to a principal components analysis which extracted seven major vegetational trends from the raw data. Stepwise multiple regressions of bird abundance at each of 19 study sites on the vegetational components demonstrated that significant proportions of the variation in abundance of 11 species out of 22 were accounted for by certain vegetational variables. An investigation of philopatry revealed that individuals of most species often returned to or near the breeding location of a previous year. For three species, a comparison of site fidelity in experienced birds and first-year adults using between season data showed that experienced birds tended to move shorter distances from a previous year's location than did first-years.

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INTRODUCTION

Habitat selection in passerine birds appears to be influenced by structural characteristics of vegetation (Hild n, 1965; James, 1971; Anderson and Shugart, 1974; Sabo, 1980, Collins et al., 1982; and others). Vegetation provides feedings areas, nesting sites, as well as song and watch posts, all of which are important stimuli eliciting species-specific responses which ensure selection of suitable habitats where species can live and reproduce.

Associations between avian community structure and vegetational configuration have been clearly documented. In some early work MacArthur and MacArthur (1961) found that by computing a foliage height diversity to describe the height profile of foliage density, they could predict bird species diversity within a given community. Several researchers (e.g. MacArthur, 1958; Parnell, 1969; Power, 1971; Morse, 1976) examined the importance of foliage preferences in birds and found that species exhibit measurable differences in selectivity for certain foliage types, thereby determining in part, the type of habitat a species occupies.

A recent move in avian ecology has been towards multivariate analysis of habitat data. In a study of habitat relationships among 46 bird species in Arkansas, James (1971) used ordination techniques to show that the distribution of a species was often closely associated with the presence of

certain structural characteristics of the vegetation. She called these characteristic vegetational requirements to which species responded the niche-gestalt, and explained that these bird-vegetational relationships are consistent and predictive in a mathematical sense. Following James a number of researchers attempted to quantitatively describe the relationships between structural characteristics of vegetation and bird abundance (Anderson and Shugart, 1974; Whitmore, 1975; Conner and Adkisson, 1977; Smith, 1977; Whitmore, 1977; Noon and Able, 1978; Anderson, 1979; Niemi and Pfanmuller, 1979; Rotenberry and Wiens, 1980; Sabo, 1980; James and Wamer, 1982; Clark et al., 1983; and others) for as Anderson and Shugart (1974) explained, the results of such studies form a basis for predicting the effects of habitat alteration upon bird communities.

It should be clear that the existence of correlation between bird abundance and vegetation configuration does not cause habitat selection. Such associations exist because the underlying life needs (food, shelter, etc.) of the bird can be satisfied, so the configuration actually represents that which is ecologically suitable for existence. The birds are responding either to measured variables, or to unmeasured parameters strongly associated with those variables (Rotenberry and Wiens, 1980; Johnson, 1981).

Although most of the recent studies of bird-habitat relationships have concentrated on habitat structure in a

general sense, some ignoring plant species altogether (e.g. Anderson and Shugart, 1974), preferential use of certain types or species of plants may be important in explaining bird distribution within habitats (Holmes, 1981). James (1971), for example, showed that within a bird's niche-gestalt, certain tree species were of particular importance. In a study conducted in the Hubbard Brook Experimental Forest, New Hampshire, Holmes and Robinson (1981) showed that passerine birds used different species of trees preferentially when foraging for insect prey with a significant departure from random in tree species use. They suggested that such preferences represent species-specific adaptations predisposing the birds to choose certain kinds of trees in which to forage, therefore the presence of certain tree species may be important in explaining distribution and abundance of some birds. While the importance of this may not have been fully appreciated in the past, they urged that future studies of forest birds must consider not just general vegetation structure, but also the particular plant species making up that structure.

Bird-habitat associations undoubtedly vary spatially and on different spatial scales. Wiens and Rotenberry (1981) studied bird-habitat relationships in shrubsteppe environments on a regional scale and compared their findings to those of a continental-scale study. They found that bird species exhibit different patterns of habitat correlation on

the two spatial scales., On a large scale, they suggested, birds are responding to characteristics of general vegetation structure while on a smaller, within habitat, scale birds may respond preferentially to certain composition and specific attributes of the vegetation. Indeed, James (1971) implies that caution should be used for fear of exaggerating the validity of her results, one reason being that the data pertained to a limited area of the breeding range of each species. Anderson (1980) stressed the need to subdivide or stratify the environment into ecoregions when attempting to associate birds with habitat structure. He reasoned that each species has its own geographic limits within which are zones of abundance representing availability of suitable habitats. Furthermore, such factors as interspecific competition, or a lack of alternative suitable habitat could alter the specificity of habitat seletion within a given local (Noon and Able, 1978).

Once a breeding habitat is chosen the individuals of many migratory species tend to return to the same breeding area in subsequent years. This behavior is called philopatry. In her Ohio study, Nice (1937) noted that male Song Sparrows, Melospiza melodia, with previous nesting experience usually returned to their former homes and that many retained the same territories year after year. Tompa (1962) found that in twenty-nine returns of fifty-five Song

Sparrows, all except one kept their territories of the previous year apart from minor boundary changes. Supportive evidence of a similar nature has been reported in other studies (e.g. Berger and Radabaugh, 1968; Catchpole, 1972; Greenwood and Harvey, 1976; Darley et al., 1977; Searcy, 1979; Abraham, 1980).

It is generally held that philopatry is a learned behavior which is strongest in older more experienced birds (Hilden, 1965; Greenwood, 1980). In Austin's (1949) study, for example, older terns, Sterna hirundo, tolerated a greater degree of habitat destruction before forsaking their nesting locations than did younger ones.

First-time breeders return to the previous year's nest locations in smaller proportions than experienced breeders. Care should be taken not to attribute this wholly to differences in site fidelity between the groups. Instead, a high probability of mortality during the first year of life (Ricklefs, 1973) largely accounts for this. For example, Baker et al. (1981) found that cohorts of White-crowned Sparrows, Zonotrichia leucophrys, experienced 70% mortality during the first year, but a constant probability of death over the rest of the lifespan. Comparisons of true site fidelity in first years and older birds, therefore should not be made on the basis of simple return rates.

Nevertheless many young birds do return to the general vicinity of their birthplace for breeding and it has been,

suggested that before first migration, they must be imprinted onto their environment. Imprinting appears to take place in the post-fledging stage, four to five weeks after having dispersed from the nest (Lohrl, 1959; cited in Hilden, 1965; Catchpole, 1972). When these young birds migrate back to the breeding ground the next spring they tend to settle where the post-fledging period had been spent the previous year, regardless of its proximity to the natal site (Catchpole, 1972; Baker, 1978).

As a consequence of juvenile dispersal, many first time breeders do not return to the natal site. The advantages of this may be to reduce intense competition between close relatives, especially at the onset of breeding, and to lower the probability of inbreeding (Horn, 1978; Greenwood, 1980; Harvey and Greenwood, 1980).

The advantages of philopatry are probably closely associated with site familiarity. Most migratory passerines are restricted in their movements as a result of establishing and defending a territory, and as Hinde (1956) explained, a territory occupant becomes familiar with the area and as a result more efficient at feeding and escaping predators there. Furthermore, returning to a suitable nest site reduced the time required to find an area and to start breeding (Baker, 1978). Searcy (1979) suggested that in Red-winged Blackbirds, Agelaius phoeniceus, the males lack reliable cues for recognizing good breeding habitat when

they set up territories at the end of winter or early spring, and may for this reason return to a former territory with which they are familiar. In a study on Blackbirds, Turdus merula, Greenwood and Harvey (1976) speculated that year to year retention of a territory is advantageous because the bird has previous experience of the variation in resource availability there and in turn, that this behavior enhances fitness. Darley et al. (1971) looked at site fidelity in Catbirds, Dumetella carolinensis, within the breeding season. They found that about one-third of the birds abandoned their territories usually after a nesting failure, but that proportionally, the reproductive success of faithful birds was greater than that of unfaithful birds. It appears that philopatry plays an important role in helping ensure that birds select habitats with optimal environments, increasing the likelihood of reproductive success thereby increasing fitness.

The current study, carried out on a community scale, will attempt to identify quantitative relationships between breeding bird distribution and habitat structure. As well, philopatry will be examined in general terms and in terms of its role in the habitat selection process. Hence, this study aims to provide necessary information for developing community management practices. If bird-vegetation relationships are for the most part consistent and systematic, then it should be possible to predict distributional pat-

terns and abundances according to the major vegetational trends within a given community. Conversely, changes in bird populations could indicate what is happening to their associated habitats. As Plunkett (1979) points out in a discussion on the importance of birds in forest communities, birds are useful as monitors of the diversity of natural biological communities, and furthermore they provide feedback which can indicate the success or failure of various management schemes.

METHODS AND MATERIALS

Study Area

The study area (45°57'N,64°14'W) lies about 11.5 km northeast of Sackville, New Brunswick and is characterized by shallow lakes, cultivated and successional fields, alder fringe along lake edges and between cultivated fields and a surrounding coniferous forest in various stages of succession. It is divided into areas A and B (Figures 1a and 1b), the former lying adjacent to the Tintamarre National Wildlife Area and the latter entirely within it.

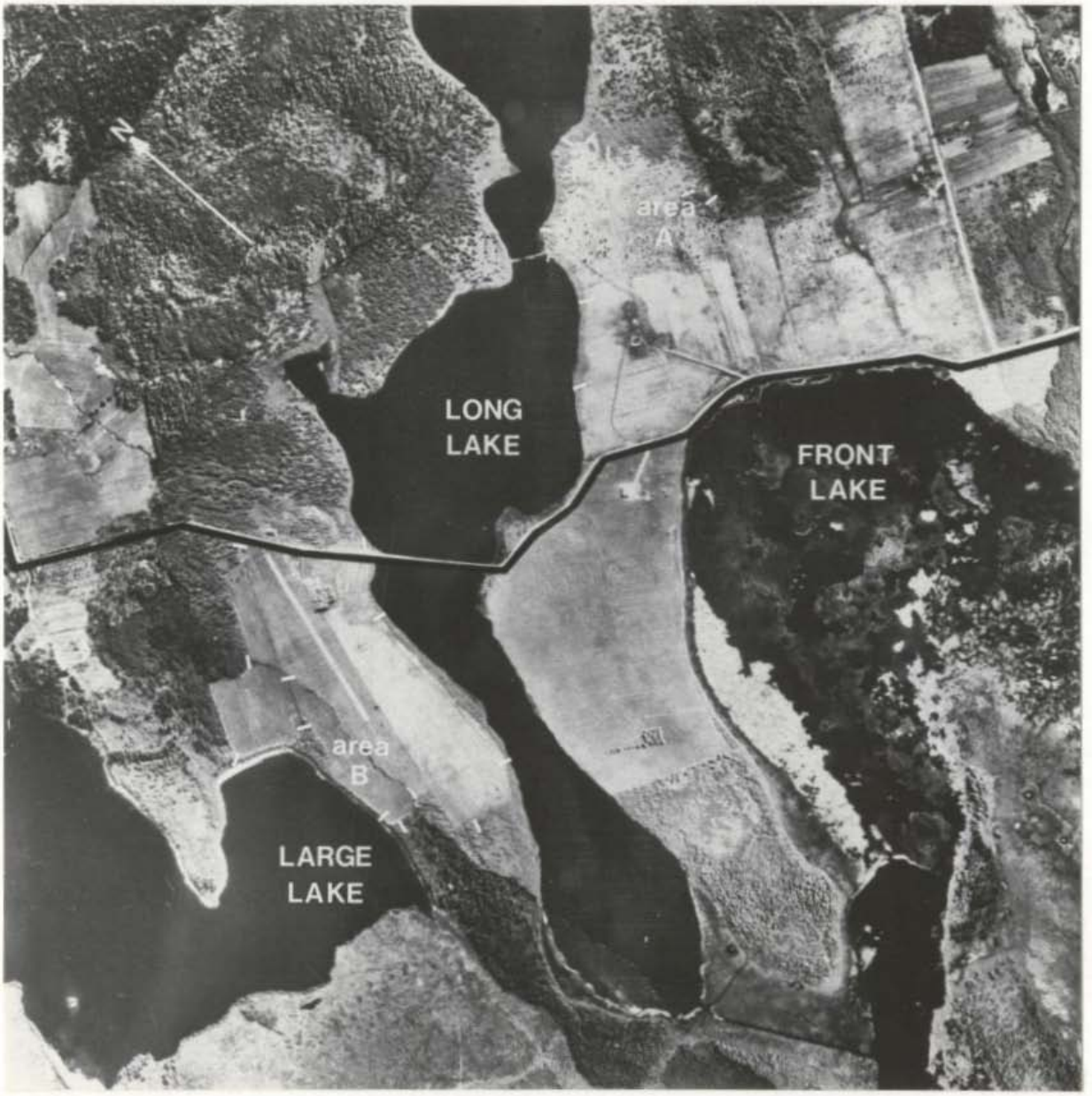
In area A, a deciduous fringe consisting mainly of alder extends along most of the lake edge merging with mixed deciduous-coniferous growth in the northeast. The remainder is largely representative of old field (secondary) succession. Area B is bounded on the lake edges by an alder dominated deciduous fringe and elsewhere by coniferous forest with some deciduous interfacing. Within this area lies a field which is cultivated annually for hay and oats. A deciduous fringe as previously described, runs through a portion of this field.

Bird Data Collection

Field work for this study was carried out from mid-May to mid-August of 1977 and 1978. Passeriform banding operations, however, had taken place in the area during several

Figure 1a. Aerial view of the study area indicating location of mist net sites. Nineteen sites are identified. Approximate scale: 1 cm = 130 m.

Figure 1b. Sketch of the study area indicating location of mist net sites. Nineteen sites are identified. Approximate scale: 1 cm = 130 m.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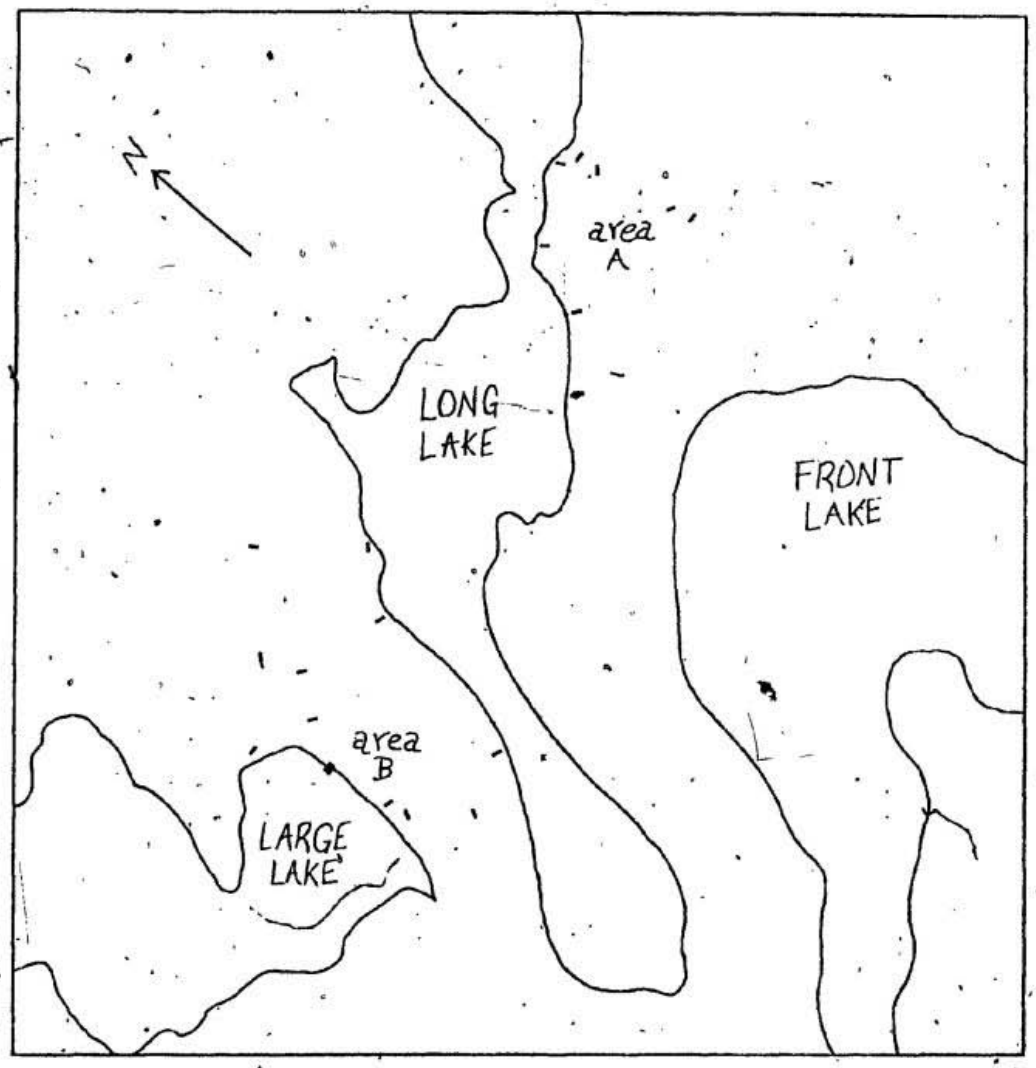
area A
LONG LAKE
FRONT LAKE
area B
LARGE LAKE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area A
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area B
LARGE LAKE

previous years.

Estimates of bird species composition were obtained through the use of Japanese mist nets. This method does not provide reliable information on true abudance, however the capture totals within each species did provide the basis for an index of abundance. Mist netting is a non-selective sampling method which gives information on the distribution of (1) a large number of species, (2) all ages, (3) both sexes, (4) breeders and non-breeders (Stamm et al., 1960). The nylon nets were fastened to 3 m aluminum poles, and when opened measured 12.5 m long by 2 m high with a 2.5 cm mesh size. Mist nets were set out in a total of 19 sites (Figures 1a and 1b). Area A was worked alternately with area B, such that all nets were open at least once weekly from early morning until early afternoon. The same net sites were used in both 1977 and 1978, with many locations exactly as in previous banding seasons (see Blacquiere, 1975). All passerines caught in the nets were taken to a centrally located field laboratory where each was identified, aged, and sexed according to Robbins et al. (1966) and Wood (1969), then banded under permit as set forth in the Migratory Bird Act, following procedures described in the North American Bird Banding Manual (1972).

Vegetation Sampling

During both field seasons, structural features of the

vegetation were measured at all mist net sites based on a method described by James (1971) and James and Shugart (1970) with several modifications to better suit the present study.

At each net site, two perpendicular arm length transects were made across a 0.04 ha circular plot centered at the midpoint of the mist net. Plants were identified according to Roland and Smith (1969), and entered into appropriate size classes as follows:

Z - 0 to 2.4 cm in diameter at breast height (DBH)

A - 2.5 to 7.4 cm DBH

B - 7.5 to 12.4 cm DBH

C - 12.5 to 18 cm DBH

D - greater than 18 cm DBH

Maximum canopy height for the circular plot was estimated using a 4.25 m pole, while estimations of canopy cover and ground cover were carried out as described in James and Shugart (1970). Nineteen vegetation variables (Table 1) were measured at each site.

Vegetation Analysis

Previous studies (see Introduction) indicate that birds may be responding to combinations of habitat variables rather than single parameters, therefore a multivariate approach was taken in vegetation analysis. Several multivariate techniques, for example polar ordination, Gaussian

Table 1: Nineteen variables of vegetation structure measured at each 0.04 ha plot.

1	ALD	Number of alder, Alnus rugosa (Du Roi), in all size classes
2	WSP	Number of white spruce, Picea glauca (Moench), in all size classes
3	BSP	Number of black spruce, Picea mariana (Mill.), in all size classes
4	APP	Number of crabapple, Pyrus Malus L., in all size classes
5	LAR	Number of larch, Larix laricina (DuRoi), in all size classes
6	CHE	Number of cherry, Prunus pensylvanica L.f., in all size classes
7	ASH	Number of mountain ash, Sorbus americana Marsh., in all size classes
8	SHA	Number of shadbush, Amelanchier spp., in all size classes
9	ASP	Number of aspen, Populus tremuloides Michx., in all size classes
10	DEA	Number of dead trees in all size classes
11	PLA	Number of all other plant species less than 2.5 cm DBH
12	Z	Number of stems less than 2.5 cm DBH
13	A	Number of stems 2.5 cm - 7.4 cm DBH
14	B	Number of stems 7.5 cm - 12.4 cm DBH
15	C	Number of stems 12.5 - 18.0 cm DBH
16	D	Number of stems greater than 18.0 cm DBH
17	%GC	Percentage ground cover
18	%CC	Percentage canopy cover
19	MCH	Maximum canopy height

analysis, reciprocal averaging and principal components analysis (PCA) may be used to reduce multidimensional data into manageable proportions. The appropriateness of each technique in relation to various types of data is presented by Gauch (1982).

PCA was the chosen method of analysis. This method is critized, though, for frequently producing distorted ordinations, with ecologically meaningless or uninterpretable axes. However, Gauch et al. (1977) suggest that PCA may be appropriate for analysing community structural characteristics as in James (1971). In view of this and for the following reasons PCA seemed appropriate: (1) it allowed reduction and simplification of the dimensionality of the original data set into a smaller set of components; (2) it produced a set of principal components that were ecologically meaningful and easily interpreted; (3) it facilitated comprehension of the relationships between variables; (4) it permitted consideration of orthogonal vegetation components in further analysis.

Analysis of Bird-Vegetation Relationships

Relationships between adult (and assumed breeding) bird abundances and structural features of the vegetation were manifested through multiple regression analyses with stepwise inclusion of the variables (principal components). This showed what percentage of the variation in species dis-

tribution among net sites can be attributed to the various vegetation differences between sites as represented by the principal components.

Bird abundances for both seasons were pooled in the analysis because (1) this resulted in a larger sample size thereby providing enough data to do valid regressions and (2) year to year variation in habitat preferences would be nearly impossible to interpret with data from just two years. Spearman rank-order correlations (Sokal and Rohlf, 1981) were carried out for species showing differential abundances among the nets to determine whether relative preference for the various sites changed from year to year.

Recapture Data Collection

Capture and recapture information from field and banding records kept from 1973 to 1978 was used to investigate site fidelity. The date, age and location of initial capture and subsequent recapture were recorded individually for (1) adult birds recaptured within the banding season, (2) adults recaptured one or more seasons after initial capture as an adult, and (3) adults recaptured for the first time one or more seasons after initial capture as a juvenile. Data were entered into these categories as distance in meters between the capture and recapture sites. If a bird was recaptured at the same site, then the distance was recorded as zero.

Analysis of Recapture Data

A breakdown by species of shifted distances by experienced adults allowed comparison of dispersal among species, both within and between seasons (categories 1 and 2 above). In addition, for those species having adequate sample sizes, Mann-Whitney rank tests and a combined probabilities test (Sokal and Rohlf, 1981) were used to test for differences in mean distances shifted by experienced and inexperienced adults between years, thereby determining whether differences could be attributed to age (experience).

Species of Birds Studied

The following 22 species of common passeriform birds are considered herein: Yellow-bellied Flycatcher, Empidonax flaviventris (Baird and Baird); Alder Flycatcher, E. alnorum Brewster; Black-capped Chickadee, Parus atricapillus Linnaeus; Gray Catbird, Dumetella carolinensis (Linnaeus); American Robin, Turdus migratorius Linnaeus; Swainson's Thrush, Catharus ustulatus (Nuttall); Red-eyed Vireo, Vireo olivaceus (Linnaeus); Black-and-white Warbler, Mniotilta varia (Linnaeus); Tennessee Warbler, Vermivora peregrina (Wilson); Yellow Warbler, Dendroica petechia (Linnaeus); Magnolia Warbler, D. magnolia (Wilson); Chestnut-sided Warbler, D. pensylvanica (Linnaeus); Wilson's Warbler, Wilsonia pusilla (Wilson); Canada Warbler, W. canadensis (Linnaeus); American Redstart, Setophaga ruticilla (Linnaeus); Rose-

breasted Grosbeak, Pheucticus ludovicianus (Linnaeus); Purple Finch, Carpodacus purpureus (Gmelin); White-throated Sparrow, Zonotrichia albicollis (Gmelin); Lincoln's Sparrow, Melospiza lincolnii (Audubon); Swamp Sparrow, M. georgiana (Latham); Song Sparrow, M. melodia (Wilson). Scientific names and authorities are according to the American Ornithologist's Union (1983).

RESULTS

Bird Census

Banding efforts in both the 1977 and 1978 field seasons yielded captures distributed throughout nearly 60 species of passeriform birds. Sample sizes within many species were extremely small, and for this reason only 22 species were considered in the investigation of relationships between breeding bird distribution and structural characteristics of the vegetation. Distribution and abundance of the adult portions of these 22 species are given in Tables 2 and 3 for 1977 and 1978, respectively.

Vegetation Analysis

Preliminary to deriving the principal components of the vegetation the data were standardized to remove units of measurement effects. A correlation matrix was then calculated for the 19 measured variables, and is presented in Table 4. All values of 'r' equal to or greater than ± 0.46 are significant at $p \leq 0.05$ with approximately 17 degrees of freedom. Although most variables were significantly correlated with at least one other, 3 variables, white spruce density (WSP), density of trees 7.5 - 12.4 cm DBH (B), and maximum canopy height (MCH) did not have any significant correlates.

To determine whether important vegetational changes oc-

Table 2. Distribution and abundance of adult birds - 1977.

Bird Species	Net Sites																			Total	% of Total
	2	3	4	5	6	7	8	9	10	11	12	14	15	16	19	20	21	22	23		
Yellow-bellied Flycatcher	1	1	1	3	1	2	0	1	0	1	1	1	2	2	0	0	2	0	1	20	3.20
Alder Flycatcher	1	4	2	1	3	1	0	1	0	6	2	3	0	3	3	0	1	0	5	36	5.77
Black-capped Chickadee	0	0	1	0	2	1	0	1	0	0	0	0	2	0	0	0	0	0	0	7	1.12
Gray Catbird	1	0	1	2	2	0	0	0	0	1	1	0	0	2	0	0	0	0	0	10	1.60
American Robin	1	1	3	3	1	2	0	3	1	2	0	3	2	1	3	3	0	2	1	32	5.13
Swainson's Thrush	3	6	4	2	5	1	2	1	0	0	0	2	4	1	1	1	3	1	2	39	6.25
Red-eyed Vireo	1	0	1	1	4	3	3	0	0	1	2	3	0	1	2	3	1	0	3	29	4.65
Black-and-white Warbler	0	1	2	0	0	0	0	2	0	0	0	1	0	0	0	0	1	0	2	9	1.44
Tennessee Warbler	0	1	3	1	2	0	0	1	0	0	1	1	0	1	2	0	1	0	0	14	2.24
Yellow Warbler	6	8	2	1	8	4	1	0	1	5	10	4	3	0	1	0	2	0	1	57	9.13
Magnolia Warbler	0	0	0	0	0	0	0	1	0	0	0	3	1	3	3	0	3	0	1	15	2.40
Chestnut-sided Warbler	0	0	0	1	1	2	1	0	0	0	1	2	3	4	0	0	0	0	5	20	3.20
Common Yellowthroat	0	0	1	2	1	2	2	1	0	3	0	2	1	1	0	3	1	1	4	25	4.01
Wilson's Warbler	2	0	0	0	2	0	0	2	0	0	0	1	1	5	5	0	0	0	1	19	3.04
Canada Warbler	0	1	0	0	3	0	0	1	0	0	1	1	2	0	0	0	0	0	1	10	1.60
American Redstart	7	9	9	2	13	4	4	7	1	4	5	8	7	3	1	3	7	1	7	102	16.35
Rose-breasted Grosbeak	0	1	1	2	1	2	1	0	1	1	1	1	2	0	3	1	0	0	0	18	2.88
Purple Finch	1	5	2	1	1	1	2	2	0	2	6	8	2	0	1	1	1	1	2	39	6.25
White-throated Sparrow	1	2	5	0	4	3	1	6	0	4	4	3	3	9	7	4	2	3	3	64	10.26
Lincoln's Sparrow	0	0	0	0	1	0	1	0	0	1	0	2	1	1	0	6	4	0	1	18	2.88
Swamp Sparrow	0	1	0	0	0	0	0	0	0	1	3	1	1	0	0	1	1	0	0	9	1.44
Song Sparrow	2	5	0	3	4	0	3	0	0	5	2	2	1	4	0	0	0	0	1	32	5.13
TOTAL	27	46	38	25	59	28	21	30	4	37	40	52	38	41	32	26	30	9	41	624	

Table 3. Distribution and abundance of adult birds - 1978.

Bird Species	Net Sites																				Total	% of Total
	2	3	4	5	6	7	8	9	10	11	12	14	15	16	19	20	21	22	23		
Yellow-bellied Flycatcher	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	6	0	0	8	2.04
Alder Flycatcher	5	5	1	4	1	4	0	0	4	3	3	3	2	5	1	3	0	0	2	46	11.73
Black-capped Chickadee	0	0	2	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	1	7	1.79
Gray Catbird	0	3	3	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	10	2.55
American Robin	0	2	1	1	1	2	0	1	4	1	1	2	0	0	2	0	0	0	0	18	4.59
Swainson's Thrush	1	2	1	1	1	1	0	0	1	0	0	1	2	1	0	1	1	0	0	14	3.57
Red-eyed Vireo	0	1	1	2	3	0	0	0	1	0	0	0	1	2	0	2	1	0	1	15	3.83
Black-and-white Warbler	1	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	6	1.53
Tennessee Warbler	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	1	0	0	5	1.28
Yellow Warbler	0	6	0	1	2	0	0	1	3	2	2	1	0	0	0	2	0	0	1	21	5.36
Magnolia Warbler	0	0	0	0	0	0	0	1	1	0	1	0	1	2	0	0	3	0	1	10	2.55
Chestnut-sided Warbler	0	0	1	0	2	0	1	0	0	0	0	1	0	1	1	0	0	0	0	7	1.79
Common Yellowthroat	0	0	0	1	0	0	1	1	1	2	2	1	1	1	2	1	1	0	0	15	3.83
Wilson's Warbler	0	1	0	1	2	1	0	2	0	1	0	1	0	1	0	1	0	0	0	11	2.81
Canada Warbler	0	0	0	1	1	0	1	0	2	0	1	0	3	0	0	0	2	0	0	11	2.81
American Redstart	4	7	4	4	11	4	2	5	4	1	3	7	1	3	7	3	7	1	0	78	19.90
Rose-breasted Grosbeak	1	1	3	1	0	0	0	0	0	1	0	1	2	0	0	0	0	0	0	10	2.55
Purple Finch	0	7	2	4	6	5	2	0	2	0	0	0	0	1	1	1	1	0	0	32	8.16
White-throated Sparrow	0	0	2	0	1	1	1	1	1	0	2	1	0	1	7	4	2	3	28		7.14
Lincoln's Sparrow	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	1	0	0	6	1.53
Swamp Sparrow	0	0	0	0	0	0	0	0	0	4	0	2	0	1	0	0	0	0	1	8	2.04
Song Sparrow	0	1	1	0	0	0	2	1	3	4	4	3	1	2	1	0	0	3	0	26	6.63
TOTAL	13	37	22	23	33	19	10	16	30	22	22	25	15	22	16	23	28	6	10	392	

Table 4. Correlation matrix (r) for 19 vegetational variables measured at 19 mist net sites. N = 38.

	ALD	WSP	BSP	APP	LAR	CHE	ASH	SHA	ASP	DEA	PLA	Z	A	B	C	D	GC	CC	MCH
ALD																			
WSP	-0.13																		
BSP	-0.09	-0.05																	
APP	-0.41	-0.02	-0.07																
LAR	-0.27	0.23	0.20	-0.11															
CHE	-0.30	0.09	-0.05	0.48*	-0.05														
ASH	-0.34	0.04	-0.07	0.44	-0.08	0.90*													
SHA	-0.30	0.24	-0.06	0.33	0.01	0.59*	0.77*												
ASP	-0.30	0.09	-0.01	-0.07	0.75*	-0.05	-0.07	0.03											
DEA	-0.08	-0.05	-0.12	-0.17	-0.11	-0.09	-0.04	-0.07	-0.13										
PLA	0.22	-0.08	-0.16	0.06	-0.17	-0.10	-0.12	-0.08	-0.10	0.30									
Z	0.56*	-0.06	-0.17	-0.09	-0.21	-0.15	-0.17	-0.11	-0.19	0.23	0.91*								
A	0.66*	-0.13	-0.06	-0.19	-0.25	-0.05	-0.08	-0.17	-0.26	0.12	0.03	0.19							
B	-0.18	0.10	0.32	-0.03	-0.05	0.14	0.06	0.05	-0.08	0.02	-0.10	-0.15	-0.17						
C	-0.38	0.26	0.61*	0.15	0.22	0.44	0.33	0.23	0.14	-0.23	-0.28	-0.35	-0.23	0.27					
D	-0.32	0.06	-0.02	-0.06	0.47*	0.02	0.05	0.16	0.36	0.51*	-0.09	-0.18	-0.06	0.15	-0.08				
GC	0.32	-0.06	0.05	-0.48*	0.06	-0.95*	-0.95*	-0.79*	0.05	0.09	0.09	0.14	0.07	-0.10	-0.37	-0.08			
CC	0.42	0.1[illegible]	-0.03	-0.23	-0.02	-0.05	-0.09	-0.11	0.10	-0.23	-0.27	-0.12	0.57*	-0.06	0.06	-0.09	0.10		
MCH	0.11	0.24	0.06	0.12	-0.15	0.24	0.13	-0.13	-0.40	-0.33	-0.12	-0.06	0.13	0.16	0.10	-0.44	-0.14	0.14	

* Significant at $p \leq 0.05$

curred at any of the 19 net sites between the 1977 and 1978 field seasons, paired t-tests were carried out using factor scores obtained in the principal components analysis (Table 5). Only one of the tests, that for site 11, was significant at $p \leq .05$ while none of the tests were significant at $p \leq .01$, indicating that the measured vegetational variables did not differ greatly between the two field seasons.

Principal components analysis was used to demonstrate that the variability in the vegetation measures among net sites is largely due to a few systematic trends in overall vegetational structure. In the analysis a new set of variables was constructed, the principal components, reducing the complexity of the initial situation so that now, a 7-dimensional space retains 82% of the information in the original data set. The residual 18% of the variance reflects random error of the vegetation measures. Table 6 summarizes the analysis and shows the extent to which the original variables are related to the principal components.

The first principal component accounts for 23.9% of the variance in the original data, with high loadings on several variables. Four deciduous species - crabapple, cherry, mountain ash and shadbush - are important here, as is the negative association with ground cover. The analysis showed that only one net site scored high on this component, indicating a unique situation characterized by the above-mentioned deciduous association and conspicuous open soil or

Table 5: Summary of paired t-tests of vegetation factor scores (paired by factor) testing for year to year variation in vegetation measurements at each net site. The factor scores were obtained in the vegetation analysis. Degrees of freedom = N - 1 = 6; D = mean difference between the paired observations; S_D = standard error of D.

Net site	D	S_D	t
2	-.22425	.316	-1.880
3	-.21520	.414	-1.377
4	-.17830	.400	-1.178
5	.03554	1.25	0.075
6	-.30334	.560	-1.434
7	.38931	.558	1.846
8	-.08367	.666	-0.332
9	.05113	1.22	0.110
10	-.13934	.253	-1.455
11	-.55003	.586	-2.485*
12	-.63532	1.15	-1.464
14	-.42400	.646	-1.735
15	-.18069	1.39	-0.345
16	-.79449	1.29	-1.630
19	-.11196	.592	-0.50
20	.6318	2.33	0.717
21	-1.0076	1.99	-1.341
22	-.51924	1.22	-1.122
23	-.15421	.551	-0.741

*significant at $p \leq 0.05$

Table 6. Summary of the results of the principal components analysis of mean values of each of 19 vegetational variables.

	Component						
	1	2	3	4	5	6	7
Percentage of total variance accounted for	23.9	15.6	12.8	9.2	7.5	7.1	5.9
Cumulative percentage of total variance accounted for	23.9	39.5	52.3	61.4	69.0	76.1	82.0
Correlations to original variables							
ALD	-0.30	-0.21	0.39	0.72	-0.16	-0.12	-0.06
WSP	0.08	0.17	-0.01	-0.02	-0.00	0.01	0.91
BSP	-0.10	0.08	-0.05	-0.00	-0.09	0.90	-0.15
APP	0.54	-0.10	-0.01	-0.40	-0.25	-0.11	-0.12
LAR	-0.07	0.85	-0.10	-0.09	0.06	0.14	0.18
CHE	0.92	-0.07	-0.06	-0.02	-0.06	0.12	0.08
ASH	0.96	-0.07	-0.08	-0.04	0.01	0.03	-0.01
SHA	0.81	0.11	-0.01	-0.08	0.11	-0.03	0.11
ASP	-0.03	0.91	-0.09	-0.07	0.03	-0.03	-0.01
DEA	-0.06	-0.17	0.21	-0.05	0.85	-0.06	-0.04
PLA	-0.04	-0.06	0.94	-0.12	0.08	-0.10	-0.04
Z	-0.10	-0.11	0.96	0.14	0.02	-0.12	-0.01
A	-0.02	-0.23	0.07	0.86	0.08	-0.09	-0.11
B	0.02	-0.25	-0.12	-0.14	0.25	0.59	0.28
C	0.34	0.21	-0.18	-0.07	-0.21	0.74	0.12
D	0.08	0.40	-0.16	-0.05	0.81	-0.01	0.02
%GC	-0.93	0.05	0.04	0.04	0.00	-0.07	-0.02
%CC	-0.04	0.12	-0.24	0.82	-0.16	-0.17	0.12
MCH	0.07	-0.45	-0.11	0.10	-0.47	0.11	0.50

rock as indicated by the high negative loading on ground cover.

A further 15.6% of the variance is explained in principal component 2. Again, just one site scored well on this component, therefore the high correlations with larch and aspen probably reflect characteristics of an extreme site. The loadings on the other variables are relatively unimportant and could reflect that areas without larch and aspen are heterogeneous for these variables, not necessarily low in them.

Principal component 3 represents 12.8% of the variance in the vegetation data and is strongly associated with density of small plants (PLA), stems of size class Z, and moderately so with alder. The associations here described situations where various small shrubs, including alder are important vegetational characteristics and where stems are generally less than 2.5 cm DBH. This third vegetational pattern emerged at a few sites as indicated by a range of factor scores.

The fourth principal component, accounting for 9.2% of the total variance, has high loadings on alder, stems of size class A, and percent canopy cover. This trend is interpreted as alder dominated shrub with stem size generally from 2.5 to 7.4 cm DBH and with a closed canopy. This latter characteristic implies that the dominant species is fairly dense, and as well that low light levels resulting

from heavy shading probably limit understory growth. There were no high factor scores on the component but three modest scores suggest that this vegetational pattern may be found intermittently throughout certain parts of the study area.

Accounting for an additional 7.5% of the total variance, principal component 5 exhibits high positive correlations with dead trees and stems greater than 18 cm DBH. A moderate negative loading on canopy height suggests that often these big dead trees had fallen over, perhaps as a result of overmaturity combined with climatic factors such as high winds. Two net sites had important factor scores on this component.

An additional 7.1% of the variance in the data is explained in component 6. A single habitat feature is emphasized here, medium sized black spruces (7.5 - 18 cm DBH). Only one site had a high factor score for this component while all other sites had scores around the origin. The important factor loadings on this component probably show characteristics of an extreme or localized situation while the other loadings reflect the fact that areas not exhibiting these special features are heterogeneous in other variables.

The seventh principal component, accounting for 5.9% of the total variance has a high loading on white spruce, and a moderate loading on maximum canopy height. Factor scores here were low with one important exception, therefore as is

the case of several other components, the vegetational attributes described here appear to be localized.

Bird Distribution - Vegetational Relationships

Spearman correlations were calculated for 13 species (Table 7) showing differential abundances among the net sites in both sampling seasons. The remaining 9 species showed relatively small differences in abundance among the nets in both years, and so were not considered in this analysis. Only one significant association was produced. Because vegetation parameters generally did not change between the two years (see Table 5) the lack of associations in relative preference for net sites probably represents random fluctuations in abundance rather than meaningful distributional patterns of the species.

Bird counts for 1977 and 1978 were combined and stepwise multiple regression analyses determined the nature and extent of relationships between bird abundance at the various net sites, and structural features of the vegetation. By this technique, the abundance of each species at the 19 net sites (dependent variables) was regressed on principal components one through seven (predictor variables). Varying combinations of the predictor variables were taken to obtain a minimum of unexplained residual variance with the smallest number of components. At each step, components that did not explain a significant amount of the residual variation were

Table 7: Summary of Spearman's rank correlations used to determine association between 1977 and 1978 species abundance rankings at the various net sites.

Species	N	Spearman's coefficient, ρ
Yellow-bellied Flycatcher	14	-0.004
Alder Flycatcher	19	0.227
American Robin	19	0.275
Swainson's Thrush	19	0.547*
Yellow Warbler	19	0.281
Chestnut-sided Warbler	10	-0.382
Wilson's Warbler	13	-0.125
American Redstart	19	0.365
Purple Finch	19	-0.307
White-throated Sparrow	19	0.271
Lincoln's Sparrow	10	0.476
Swamp Sparrow	9	-0.417
Song Sparrow	16	0.067

* significant at $p \leq 0.05$

dropped (Sokal and Rohlf, 1981).

The regression analyses are summarized in Table 8. Included in the table are multiple correlation coefficients (Multiple R) and coefficients of determination (R^2). Multiple R is a measure of linear correlation between the dependent variable and the predicted values from the regression, here bird distribution and structural features of the vegetation. The absolute value of R indicates the relative strength of the relationship. R^2 gives a more direct interpretation of the strength of the relationship than does Multiple R, because it is a measure of the proportion of variance in bird distribution explained by the vegetational variables. Note that Multiple R and R^2 values are cumulative with the step-wise inclusion of the predictor variables. Also found in Table 6 are values for two significance tests: "F of step" and "Overall F." The former tests the independent contribution of each vegetational component as it is taken into the regression, and the latter tests the multiple correlation value to determine whether it is real or due to chance or error.

Bird species abundance regressed on vegetational components demonstrated that significant portions of the distribution of 11 of the 22 species can be attributed to structural features of the vegetation as represented by the principal components. The summarized results are straight-forward and easily interpreted. For example, 25%

Table 8. Summary of stepwise multiple regressions of bird species abundance on the principal components. Summaries are presented only for those species significantly related to at least one principal component. Degrees of freedom for "F of Step" = 1 and N-k-1, and for "Overall F" = k and N-k-1 where N = number of cases = 19 and k = number of independent variables.

Species	Step	Variable	Multiple R	R^2	F of Step	Overall F
Yellow-bellied Flycatcher	1	PC5	0.56	0.31	16.33*	16.33*
Swainson's Thrush	1	PC3	0.40	0.16	6.85*	6.85*
Black-and-white Warbler	1	PC1	0.39	0.15	6.41*	6.41*
Yellow Warbler	1	PC3	0.50	0.25	11.72*	11.72*
	2	PC5	0.61	0.37	6.89*	10.26*
Magnolia Warbler	1	PC6	0.39	0.15	6.52*	6.52*
	2	PC7	0.50	0.25	4.70*	5.95*
Chestnut-sided Warbler	1	PC5	0.58	0.27	13.25*	13.25*
Canada Warbler	1	PC4	0.43	0.18	7.95*	7.95*
American Redstart	1	PC3	0.41	0.17	7.29*	7.29*
Rose-breasted Grosbeak	1	PC4	0.43	0.18	7.95*	7.95*
White-throated Sparrow	1	PC5	0.56	0.32	16.76*	16.76*
Lincoln's Sparrow	1	PC7	0.42	0.17	7.61*	7.61*

* Values are significant at $p \leq 0.05$.

of the variability in the distribution of Yellow Warblers was attributable to component 3, and a further 12% attributable to component 5.

A log likelihood ratio, goodness of fit test (Sokal and Rohlf, 1981), carried out for each species showed no difference between the observed abundance at each net site and that predicted by the regression (see Table 9).

Finally, since abundances fluctuated greatly between some species the likelihood of significant regressions occuring more frequently with more abundant species than less abundant species was determined. Counts for the two years were combined and a contingency test on median split in abundances and number of significant regressions showed no significant difference between the two abundance categories at $p \leq 0.05$ (Table 10).

Site Fidelity

Capture and recapture totals (1973-77 and 1974-78 respectively) for the 22 bird species are presented in Table 11. Recapture totals include all individuals of a species returning to the study area in a year subsequent to that of banding; multiple returns by an individual are not included as such, but simply count as one. Recapture rates range from 0.0% for Black-and-white Warblers, Tennessee Warblers, Magnolia Warblers and Canada Warblers to 12.1% for Chestnut sided Warblers.

Table 9: Summary of log likelihood ratio, goodness of fit test for differences between the observed abundance of each species at each net site, and that predicted by the regression ($p \leq 0.05$).

Species	Degrees of Freedom	Log-likelihood Ratio	
Yellow-bellied Flycatcher	5	.08	n.s.
Alder Flycatcher	13	1.74	n.s.
Black-capped Chickadee	2	2.29	n.s.
Gray Catbird	4	.74	n.s.
American Robin	10	.87	n.s.
Swainson's Thrush	9	3.48	n.s.
Red-eyed Vireo	7	.700	n.s.
Black-and-white Warbler	2	.55	n.s.
Tennessee Warbler	3	.45	n.s.
Yellow Warbler	10	13.60	n.s.
Magnolia Warbler	4	1.20	n.s.
Chestnut-sided Warbler	5	.86	n.s.
Common Yellowthroat	7	.66	n.s.
Wilson's Warbler	5	.63	n.s.
Canada Warbler	4	2.41	n.s.
American Redstart	18	10.40	n.s.
Rose-breasted Grosbeak	6	1.42	n.s.
Purple Finch	13	21.92	n.s.
White-throated Sparrow	12	3.83	n.s.
Lincoln's Sparrow	4	1.37	n.s.
Swamp Sparrow	2	.30	n.s.
Song Sparrow	10	2.48	n.s.

Table 10: Contingency table and Chi-square test to determine if rarer species tend to have poorly predicted vegetation associations in the regression.

	Abundance ≥ 30	Abundance < 30	Totals
Regressions Significant	4 (5.5)*	7 (5.5)*	11
Regressions Not Significant	7 (5.5)*	4 (5.5)*	11
Totals	11	11	22

* expected frequencies

Degrees of freedom = 1

χ^2 = 1.64 (not significant at $p \leq .05$)

Table 11: Banding and recapture totals for the period 1973-1978.

Species	Banding Totals 1973-1977	Recaptures 1974-1978 Totals	%
Yellow-bellied Flycatcher	68	5	7.4
Alder Flycatcher	178	21	11.8
Black-capped Chickadee	63	1	1.6
Gray Catbird	85	4	4.7
American Robin	191	13	6.8
Swainson's Thrush	300	15	5.0
Red-eyed Vireo	136	14	10.3
Black-and-white Warbler	32	0	0.0
Tennessee Warbler	274	0	0.0
Yellow Warbler	325	20	6.2
Magnolia Warbler	69	0	0.0
Chestnut-sided Warbler	58	7	12.1
Common Yellowthroat	126	7	5.6
Wilson's Warbler	69	5	7.2
Canada Warbler	60	0	0.0
American Redstart	411	18	4.4
Rose-breasted Grosbeak	58	4	6.9
Purple Finch	134	9	6.7
White-throated Sparrow	295	23	7.8
Lincoln's Sparrow	99	7	7.1
Swamp Sparrow	150	2	1.3
Song Sparrow	531	35	6.6

A further breakdown giving approximate distances that adult birds moved between capture and recapture sites allowed dispersal comparisons between species, both between and within years (Tables 12 and 13). To assist interpretation of these results, Table 14 provides a breakdown of the 171 possible internet distances into the "distance shifted" categories of the preceeding two tables. Table 12 gives the distribution of adults in relation to their original capture sites in a previous year. In 3 species, American Robin, Yellow Warbler and Chestnut-sided Warbler, 50% or more of the individuals were recaptured at their original capture sites. Eighty percent or more of the individuals in 14 of 18 species were recaptured within 400m (86% of the total number of individuals irrespective of species), indicating a trend to return to a familiar area. Dispersal of adults within a breeding season was examined and as seen in Table 13, many individuals (45% of total) apparently did not shift sites at all. In 16 of 19 species 80% or more of the individuals (or 90% of the total number of individuals - all species) were recaptured within 400m of the first capture site. Hence, the tendency to keep within a small, familiar area was again apparent for both the between and within year recaptures. In conjunction with this the distribution of internet distances (Table 14) further supports site fidelity here. Approximately 47% of all possible internet distances were greater than 800 m yet only 10% and 14% of the indivi-

Table 12. Site fidelity of adult birds between breeding seasons.

Species		Distance Shifted (m)					Mean Distance (m)
		0	0-200	200-400	400-800	>800	
Yellow-bellied Flycatcher	No.	1	1	1	-	-	138
(3)	%	33	33	33	-	-	
Alder Flycatcher	No.	1	5	1	1	-	144
(8)	%	12	62	12	12	-	
Black-capped Chickadee	No.	-	-	1	-	-	360
(1)	%	-	-	100	-	-	
Gray Catbird	No.	-	-	1	-	-	225
(1)	%	-	-	100	-	-	
American Robin	No.	2	-	1	-	-	85
(3)	%	67	-	33	-	-	
Swainson's Thrush	No.	2	4	2	-	-	144
(8)	%	25	50	25	-	-	
Red-eyed Vireo	No.	2	1	2	2	1	354
(8)	%	25	12	25	25	12	
Yellow Warbler	No.	8	4	3	-	-	96
(15)	%	53	27	20	-	-	
Chestnut-sided Warbler	No.	-	4	1	1	1	355
(7)	%	-	57	14	14	14	
Common Yellowthroat	No.	2	-	2	-	-	145
(4)	%	50	-	50	-	-	
Wilson's Warbler	No.	1	1	2	-	1	329
(5)	%	20	20	40	-	20	
American Redstart	No.	-	5	3	-	4	517
(12)	%	-	42	25	-	33	
White-throated Sparrow	No.	2	10	4	3	-	216
(19)	%	10	53	21	16	-	
Rose-breasted Grosbeak	No.	0	2	1	-	-	227
(3)	%	-	67	33	-	-	
Purple Finch	No.	0	2	2	1	1	390
(6)	%	-	33	33	17	17	
Lincoln's Sparrow	No.	1	3	1	-	-	138
(5)	%	20	60	20	-	-	
Swamp Sparrow	No.	0	1	-	-	-	105
(1)	%	-	100	-	-	-	
Song Sparrow	No.	5	5	2	1	-	136
(13)	%	38	38	15	8	-	
All Species	No.	27	48	30	9	8	260
(122)	%	22	39	25	7	7	

Table 13. Site fidelity of adult birds within a breeding season.

Species		Distance Shifted (m) 0	0-200	200-400	400-800	>800	Mean Distance (m)
Yellow-bellied Flycatcher	No.	8	9	1	-	-	82
(18)	%	44	50	6	-	-	
Alder Flycatcher	No.	18	2	-	-	1	53
(21)	%	86	9	-	-	5	
Black-capped Chickadee	No.	1	2	1	-	-	157
(4)	%	25	50	25	-	-	
Gray Catbird	No.	2	1	1	1	4	504
(9)	%	22	11	11	11	44	
American Robin	No.	4	1	3	1	-	177
(9)	%	45	11	33	11	-	
Swainson's Thrush	No.	5	8	3	-	1	172
(17)	%	29	47	18	-	6	
Red-eyed Vireo	No.	2	8	4	1	2	257
(17)	%	12	47	23	6	12	
Tennessee Warbler	No.	-	2	-	-	1	495
(3)	%	-	67	-	-	33	
Yellow Warbler	No.	25	9	5	2	4	166
(45)	%	56	20	11	4	9	
Magnolia Warbler	No.	-	3	-	-	-	60
(3)	%	-	100	-	-	-	
Chestnut-sided Warbler	No.	4	5	1	-	1	200
(11)	%	36	45	9	-	9	
Common Yellowthroat	No.	7	4	1	-	-	82
(12)	%	58	33	8	-	-	
Wilson's Warbler	No.	-	3	1	-	-	186
(4)	%	-	75	25	-	-	
American Redstart	No.	10	9	2	3	1	190
(25)	%	40	36	8	12	4	
Purple Finch	No.	-	-	2	-	1	588
(3)	%	-	-	66	-	33	
White-throated Sparrow	No.	14	12	3	1	1	143
(31)	%	45	39	10	3	3	
Lincoln's Sparrow	No.	5	2	-	-	-	36
(7)	%	71	29	-	-	-	
Swamp Sparrow	No.	2	-	-	-	-	0
(2)	%	100	-	-	-	-	
Song Sparrow	No.	23	15	2	2	1	102
(43)	%	53	35	5	5	2	
All Species	No.	130	96	30	11	18	159
(284)	%	46	33	11	4	6	

Table 14: Distribution of internet distances.

	Distance Categories			
	0-200	200-400	400-500	800
No. of internet distances in each category	25	39	26	81
% of total (approx.)	15%	23%	15%	47%

duals in the within and between year categories respectively shifted differences greater than this.

It should be pointed out that, based on initial capture positions, it might be much easier for some birds to be recaptured close to "home" than it is for others. In an area where nets are clustered (see Figure 1b) the probability of a close recapture is greater than the probability of a close recapture in an area of less clustered or more isolated nets. This has therefore created a subtle problem with regard to the capture-recapture measures. Since the actual probability of recapture could not be calculated for every species of every net site the interval form (i.e. 0-200m, 200-400m etc.) of presenting recapture or dispersal distances largely eliminates ambiguity and facilitates straightforward comparisons between species.

Finally, using the recapture information, an attempt was made to determine whether older, experienced birds have a greater tendency to return near a previous year's capture site than first year adults breeding for the first time. Sample sizes in the first year adults were generally small, therefore only those species with more than two entries in this category were considered here. This permitted analyses on just three species, Swainson's Thrush, Yellow Warbler and Song Sparrow. Mann-Whitney 2-sample rank tests and a combined probabilities test were used to test for difference in distances moved by birds in the two categories (Table 15).

Table 15: Summary of Mann-Whitney tests and a combined probabilities test to determine whether shorter distances were moved by experienced adults$_{(1)}$ than first-year adults$_{(2)}$ between years ($p \leq 0.05$).

Mann-Whitney Test		P	lnP
1. Swainson's Thrush			
$n_1 = 8$	$median_1 = 137.5$ m		
$n_2 = 7$	$median_2 = 375.0$ m		
$W = 52.0$		0.1832(n.s.)	-1.6972
2. Yellow Warbler			
$n_1 = 15$	$median_1 = 0.0$ m		
$n_2 = 4$	$median_2 = 597.5$ m		
$W = 133.0$		0.0989(n.s.)	-2.3136
3. Song Sparrow			
$n_1 = 13$	$median_1 = 90.0$ m		
$n_2 = 8$	$median_2 = 175.0$ m		
$W = 129.0$		0.3282(n.s.)	-1.1141
TOTAL			-5.1249

$-2\Sigma lnP = -2(-5.1249) = 10.2498$; Degrees of freedom = 6

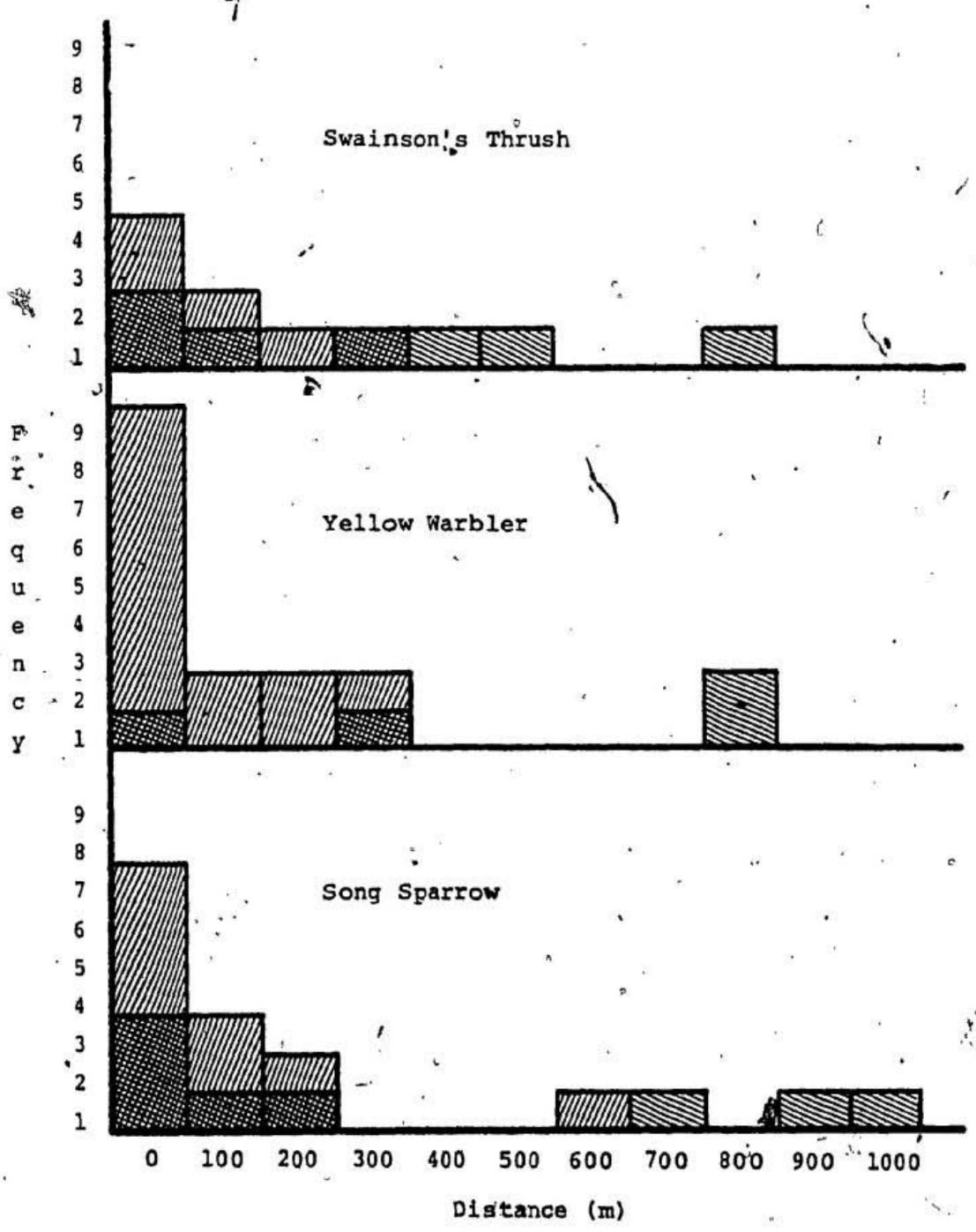
Conclusion of combined probabilities test: The difference is significant at $p \leq 0.05$.

Median distances were determined and for all three species first year adults tended to be captured farther away from the initial capture site than did experienced adults. According to the Mann-Whitney tests, however, these distances were not significantly different probably because there was a great amount of overlap in the distance measurements between the two categories. Frequency distributions of distances showed this in Figure 2. Another test combining the probabilities obtained in the independent Mann-Whitneys did show a significant difference between the distances moved by experienced birds and first year adults (Table 15).

Figure 2. Frequency distributions of distances moved by adults and first-year adults between years.

 - adults

 - first-year adults


Swainson's Thrush
Yellow Warbler
Song Sparrow
Frequency
9
8
7
6
5
4
3
2
1
0
100
200
300
400
500
600
700
800
900
1000
Distance (m)

DISCUSSION

Bird species distribution among the various net sites was based directly on mist netting captures. The capture information may not have reflected the true abundance of the species but nevertheless did provide an index of abundance and in turn an index to habitat suitability. Between species abundance comparisons were not made, therefore possible species selectivity attributable to the netting technique was irrelevant.

Seven major independent vegetational trends were identified across the net sites through the use of principal components analysis. Principal components 1, 2, 5, 6, and 7 were fairly localized, each determined largely by vegetational measurements at just one or two net sites. Principal components 3 and 4, on the other hand, represented more widespread trends in overall vegetational structure.

When bird species abundance was examined in relation to each of the principal components, significant vegetation associations showed up for 11 species.

Principal component 1 was a useful predictor for just one species, the Black-and-white Warbler, accounting for 15% of the variation in the distribution of this species. This component represents a mixed-deciduous habitat with a tree species composition unique among the net sites. Because a number of variables are emphasized here, a nearly complete

picture of a localized habitat emerges. PC 1 stands alone in this respect: Since Black-and-white Warbler distribution is correlated with this component and uncorrelated with any other, the predictable portion of this species' distribution is correspondingly localized to PC1-type habitat attributes. Typical descriptions of this species' habitat include deciduous and mixed woodlands (Bent, 1963; Godfrey, 1966), hence the quantitative associates produced in this study support those more qualitative in nature.

None of the bird species were significantly associated with principal component 2. Like PC1, this component emerged as a result of unusual measurements at just one site. Here, however larch and aspen are the only important contributing variables, unlike the situation in PC1. It might be speculated that PC2 is too extreme for any bird species considered here. Larch and aspen were especially important on just one site, but perhaps overall occurrence was too low to attract birds otherwise associated with higher densities of these trees. While this could be one explanation for PC2's failure to predict bird distribution, this is not to say that birds are not attracted to certain features offered by larch and aspen. Individual birds may regularly visit these trees (for foraging, nesting, etc.) as part of the available habitat, but if this use is not on a selective or differential basis over other tree species, predictive bird-vegetational relationships would not be expected to

show up.

Bird species associations with principal components 3 and 4 will be considered next. The distributional patterns of Swainson's Thrushes Yellow Warblers and American Redstarts were related to PC3. This component has been described as representing young shrub, probably dominated by alder, and characterized the vegetational structure at several net sites. These findings satisfactorily compare with descriptive accounts associating Swainson's Thrushes with tall deciduous shrubbery or thickets (Bent, 1964; Godfrey, 1966), Yellow Warblers with open, shrubby growth (Bent, 1963; Godfrey, 1966) as described here and American Redstarts with deciduous woods and shrubby forest edges (Ficken, 1962; Morse; 1973).

Principal component 4 also describes shrub, but here it is well developed and alder dominated with a fairly closed canopy layer. It was important throughout parts of the study area. Eighteen percent of the variation in the distributional patterns of both Canada Warblers and Rose-breasted Grosbeaks were associated with this component. Descriptions of habitats of Canada Warblers indicate that these birds are most likely to be found in shrubby undergrowth of deciduous forests, or in tall deciduous shrub near moist places (Bent, 1963; Godfrey, 1966). Rose-breasted Grosbeaks are usually considered birds of deciduous or mixed and second-growth woodlands (Godfrey, 1966; Bent, 1968).

The bird-vegetational correlations found here generally appear to support these qualitative descriptions. While PC3 and PC4 are independent vegetational patterns, it is suggested that PC3 may represent a stage in a successional sequence that will in time grow into PC4-type vegetation. If this is so, then here is an example of bird-habitat associations being separated out at particular successional stages of the vegetation.

Turning to principal component 5, the vegetation analysis indicated that large dead trees were an important physionomic characteristic in just a couple of sites. The distributional pattern of Yellow Warblers was related independently to both PC3 and PC5; and the distributional patterns of Yellow-bellied Flycatchers, Chestnut-sided Warblers, and White-throated Sparrows were related to the latter component alone. The Yellow Warbler is quite typically associated with open, shrubby growth as mentioned during the discussion of its association with PC3, and the Yellow-bellied Flycatcher is usually considered a bird of shady thickets and woodlands or a combination of the two (Godfrey, 1966). The Chestnut-sided Warbler is often reported to be found in open, mainly deciduous, bushy growth and edges of woods (Bent, 1963; Godfrey, 1966) and the White-throated Sparrow is generally considered an inhabitant of open young thickets and bushy openings in woodlands (Godfrey, 1966; Bent, 1968). The bird-vegetational correlations found here do not appear

to support these qualitative descriptions, but perhaps there is no contradiction implied, either. It is important to consider that PC5 emphasizes a single habitat feature - dead trees. The presence of these dead trees seems to suggest in itself the existence of other surrounding trees, though type or state of maturity is unknown.

Principal components 6 and 7 each emphasized a single habitat attribute, medium sized black spruces and relatively tall white spruces, respectively. In addition both conditions were localized. While the trends represented by these two components were separate and independent, they do express a common feature - spruce trees. Although these two spruces are usually characteristic of somewhat different moisture gradients, the structural features of the two are very similar. Twenty-five percent of the variability in the distribution of Magnolia Warblers was attributed to these components (15% and 10% respectively). It may be that the coniferous element itself, not necessarily the particular tree species, is more important to these birds. Lincoln's Sparrows, on the other hand, were associated with white spruce (PC7) but not black spruce (PC6) at least within the limits of this analysis. In this case it is suggested that the actual tree species is of particular importance in predicting bird distribution. Magnolia Warblers are typically associated with young or low spruce woods and edges (Bent, 1963; Morse, 1976) and rarely found outside

coniferous habitat (Greenberg, 1979). Lincoln's Sparrow too, is often found among low or stunted coniferous growth (Godfrey, 1966; Bent, 1968).

In this study, several species were shown to reflect the same habitat preferences. This results in interspecific habitat overlap which in turn can result in competition. The degree of competition depends on the extent to which species utilize the same resources, and of course the state of the resources in question (Pianka, 1983). Interspecific competition and resource overlap would be expected to be greatest among similar species (closely related on the basis of phylogeny or life habits and requirements) and when resources are limited. Guild structure has been useful in assessing resource partitioning and competition (Willson, 1974; Holmes et al., 1979; Rice et al., 1983). Greater resource overlap should occur among species within guilds than among species of different guilds (Landres and MacMahon, 1983). Wiens (1977) however states that broad resource overlap could instead indicate an abundance of resources and reduced competition. It was not the objective of this study to analyse resource state or availabilty and resource partitioning among the various species. Hence, further discussion concerning either competition or the lack of it regarding those species exhibiting habitat overlap cannot be justified.

Correlations of vegetational features with distribu-

tional patterns of 11 bird species were demonstrated. A general consideration of these relationships revealed that the greatest number of associations and the strongest correlations were with PC5. The importance of this component relative to the others is not readily explained. Though not especially widespread, this component emphasized an interesting habitat parameter - large dead trees. It might be speculated that the large dead trees were not as important to the birds as were other unidentified aspects of habitat in these areas.

Overall it appeared that components representing more generalized parameters (eg. PC 3, 4 and 5) were somewhat better predictors of bird species distribution than components emphasizing a single habitat feature (e.g. PC 2 and 6), at least in this study. In addition the success of a component in predicting species distributions appeared independent of whether the vegetational trend in question was localized or widespread.

Two of the best predictors, PC3 and 4, were the ones on which the net sites were more evenly ordinated in contrast to the others. This implies that some of the superiority of these components as predictors of bird abundance is due to this fact, especially as linear regression was used to extract the bird-vegetation relationships. While the underlying biology is not in question here, it is cautioned that the importance of the relationships could be over-emphasized

due to the mathematics involved. Furthermore, some of the differences among the principal components generally, in their value as predictor variables is undoubtedly related to the mathematics.

The vegetation analysis did not single out any individual variables as being especially important. As a group, it was clear that the variables representing stem density within various size classes were well chosen because in 9 of the 11 bird-vegetation relationships, these variables emerged as major contributors.

Until recently it had been widely accepted that general habitat structure was more important than floristics in explaining quantitative bird-habitat relationships. Lately though, some studies have suggested that knowledge of plant species composition in addition to physionomics may be useful in many instances (e.g. Holmes and Robinson, 1981; Wiens and Rotenberry, 1981; Rice et al., 1983). In this study the importance of floristics in describing habitat associations of birds was obvious. Nine of the nineteen vegetational variables dealt with plant species composition and abundance. In PC1, for example, high loadings in 4 plant species contributed to the most complete habitat picture of all the components, thereby identifying several floristic elements important in explaining Black-and-white Warbler distribution. Floristic composition was also important in 5 other bird-vegetation correlations.

Mathematical relationships were found correlating the distributional patterns of some birds to some vegetational variables. While significant habitat correlations were produced for 11 bird species, large portions of the variation still remains unaccounted for. In addition no significant correlations could be shown at all for 11 other species. A number of explanations, singly or in combination, could account for this. Avian sample sizes fluctuated a great deal between species. A Chi-square test to determine whether more abundant species were more likely to produce significant regressions than less abundant species showed no significant difference (Table 10). However, perhaps the range of abundances among the net sites was not adequate to allow for the differentiation between actual relationships and error in the regression.

The year-to-year variation in species abundances imposes limitations on the methodology. The Purple Finch, for example, is one of the more abundant species in both years. Each year it has a distinctly uneven distribution among the net sites and relatively high abundance at some sites. However the sites associated with high abundance are not the same ones in both years. It well may be that if each year's data was treated separately, significant but different vegetational relationships might have shown up. The pooled abundances have probably greatly affected the regression results such that no vegetational preferences were discern-

able for this species.

Undoubtedly some vegetational relationships were missed because some birds were responding to vegetational patterns other than those identified in this study. There are two possibilities here. First, consider that the principal components represent special combinations of the original vegetation variables. A bird species could be responding to some of these variables but not to the particular combinations represented in the principal components - hence, the birds have shown up but the relationships have not. Secondly, some species might be responding to vegetation variables that were not even considered in this study.

Intrinsic peculiarities of species sometimes defy general rules used in explaining or predicting certain phenomena. While mathematics was a useful tool in helping uncover bird-vegetation associations here, some of these associations could have been missed because of poor fit of species responses to linear vegetation trends. Consider for example, that between certain maximum and minimum values for a particular vegetation feature, a species may respond linearly, but above and below these values respectively, responses could be non-linear. In this instance the poor fit to the linear predictor fails to reveal any relationship at all.

For some species the absence of habitat correlations results from an indifferent response to the vegetation vari-

ables. These species are probably not as restricted in habitat choices by vegetational parameters, as are previously considered species which do show preferences. Such species, found throughout a variety of habitats, may be considered more generalized than the others and thus more flexible in their ecological requirements (MacArthur, 1958). As a result these more generalized species would be more resilient to factors such as habitat deterioration than species which are somewhat specialized.

In many species of birds habitat selection can be influenced by philopatry. In this study philopatry was exhibited by most of the species considered. Adult birds returning to the breeding grounds often returned to their old sites or took up new sites nearby, for the most part (Table 12). In addition birds recaptured within a particular breeding season generally showed low levels of dispersal (Table 13).

An overall 61% of returning experienced breeders returned to within 200 m of their original capture sites of a previous year (Table 12). Of the 122 individuals belonging to 18 species, the mean overall distance moved from the original capture site was 260 m (range: 85m - 517m). Clearly, philopatry is an important factor influencing habitat selection in these birds.

It has already been demonstrated in this study that some birds preferentially cue in to certain vegetational

characteristics in selecting a breeding site. In fact numerous studies during the past decade have attempted to mathematically describe bird-habitat relationships. It is possible that if site fidelity is strong enough it could alter a seemingly species-typical response. If advantages conferred by remaining faithful to a familiar spot outweigh those of moving to someplace typical but new and unfamiliar this behavior should be selected for in a population. In terms of habitat physionomy, the extent to which site fidelity will keep an individual from a species-typical habitat was beyond the scope of this study but as Hilden (1965) carefully pointed out, "optimal environment" does not always have to mean the one where an individual would seem to be most fit.

Consider the generalist versus specialist groups with regard to vegetational requirements within the habitat. This is speculative, but the former probably has more to gain by being site faithful than the latter. Assuming that the specialist by definition is correlated with and dependant upon certain vegetational requirements, in the face of physionomic habitat deterioration, dispersal to a more suitable location would be necessitated. The generalist, however, could probably adapt to a changing environment and would frequently be better off remaining faithful than moving out.

It would be interesting to test this idea in habitats

where overall vegetational structure changed significantly though not drastically, over one or more breeding seasons, such as described by Whitmore (1979). For example, vegetational changes could result from the forest management technique known as shelterwood cutting. A suitably large study area could be selected to include a shelterwood cut and surrounding forest. A capture-recapture program could be conducted and for each returning individual the distance from a previous year's breeding site in the shelterwood cut could be measured. In an attempt to select an optimal site, specialists would be expected to disperse farther (i.e. into the species-typical undisturbed forest) than generalists in search of a suitable breeding location.

Philopatry is believed to be less well developed in young birds breeding for the first time than in older more experienced individuals. A trend in the result of this study would seem to support this idea but unfortunately statistical analysis regarding this was beset with two major problems. First of all, recaptures of first-year adults were so low that only Swainson's Thrushes, Yellow Warblers, and Song Sparrows were justifiably considered here. Secondly, overlap in the distance measurements between experienced birds and first-year adults was so great that the Mann-Whitney tests (Table 15) could not produce significantly different distances for the two groups even though median distances seemed far apart, and a visual inspection of

distances supports the trend for all three species (Figure 2). The probabilities obtained in the Mann-Whitney tests were low enough to consider combining them in an overall significance test (Table 15). The results of the combined probabilities test statistically supported the contention that experienced birds are more site faithful than first-year adults at least in terms of distance moved from a previous year's site.

Juvenile dispersal seems to be important in explaining why fewer first-time breeders returned to the previous year's nesting site than experienced breeders. Juvenile dispersal occurs when the young birds are several weeks old; they leave the natal site and move out into a presumably less crowded space usually within the general area (Hilden, 1965). If the process of imprinting takes place after dispersal from the natal site then the young birds, upon return migration, would be expected to settle in a familiar area, probably where imprinting had occurred the previous year.

Another explanation for greater dispersal in young birds than older birds is that a young bird attempting to return to the previous year's site might be forced out by returning parents they cannot displace. The young bird therefore may have no choice but to disperse farther as long as a parent holds the territory.

Vegetation, as the basis of the food chain, is also the basis of habitat. The success of any bird species within a

particular habitat depends on whether essential needs are available there. For most birds, vegetational components of the habitat, directly or indirectly, indicate whether many of these needs can be satisfied. In this study 11 bird species were correlated with vegetational habitat features. In the habitat selection process it seems likely that philopatry operates initially during migration back to the breeding grounds, such that individuals tend to return to familiar areas. Then it seems that the selection mechanisms for a suitable nesting site take over until a territory is taken. Varying levels of site fidelity may operate here, depending on the age of the individual and how specific its habitat requirements are. One thing is clear, although species-typical habitat associations of some birds may be mathematically defined, it is difficult to similarly assess the importance of a behaviour such as site fidelity. While mathematical bird-habitat relationships are extremely useful in community management practices, the potential effect of site fidelity on altering these relationships deserves some consideration.

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